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ECOLOGY, POPULATION BIOLOGY AND MORTALITY OF *EUPTOIETA HEGESIA* CRAMER (NYMPHALIDAE) ON JAMAICA

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ABSTRACT. We examine the ecology, population biology and potential sources of mortality of *Euptoieta hegesia*, a tropical lowland butterfly from Jamaica, using a combination of captive rearing, studies of natural populations, and experimental approaches. We provide detailed observations of the life cycle and methods for captive rearing of this species. We assess the relative performance of larvae on primary and secondary hostplants, distribution of larvae on the primary hostplant, hostplant population utilization, and the distribution of *E. hegesia* on the island. A mark-release-recapture study was conducted to estimate population parameters and we recorded sex, size, age (as estimated by wing wear), and wing damage sustained by the butterflies prior to their initial capture. We provide evidence that *Turnera ulmifolia* is the primary hostplant of *E. hegesia* on Jamaica and that butterfly population size is not limited by the availability of hostplants. These short-lived butterflies appear to be residents of discrete hostplant populations and experience high mortality levels. Females are damaged more frequently, show more total damage and more frequent symmetrical hindwing damage (attributable to ground-based predators) than do males. We compare the results of the population study with available studies of other tropical butterflies and suggest that lowland butterfly population structure and dynamics are significantly different from that of rainforest species.

Additional key words: tropical lowland habitats, *Turnera ulmifolia*, cyanogenesis, sexual dimorphism, predation.

Euptoieta hegesia Cramer (Nymphalidae) uses *Turnera ulmifolia* L. (Turneraceae) as its primary hostplant on the island of Jamaica in addition to several *Passiflora* spp. (Passifloraceae) to a lesser degree (see below). *Turnera ulmifolia* is known to exhibit extensive genetically-based variation for a putative defense trait, cyanogenesis (the ability of plants to liberate hydrogen cyanide upon damage to tissues), within and between populations on Jamaica (Schappert & Shore 1995) whereas the Jamaican species of *Passiflora* which have been investigated are uniformly cyanogenic (Spencer 1988, Schappert & Shore, unpubl. data). Our ongoing studies of the *T. ulmifolia–E. hegesia* hostplant-herbivore system are centered on this variation in the ability of the hostplant to liberate hydrogen cyanide and the interaction with *E. hegesia*. In the long term, we hope to investigate the strength of selection imposed by both organisms, one upon the other. For example, we are finding that the

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magnitude of cyanogenesis exhibited by the hostplant has little or no effect on the growth and development of *E. hegesia* larvae (Schappert & Shore, unpubl. data), suggesting that this species is capable of detoxifying and/or sequestering cyanogenic glycosides, perhaps for their own chemical defense.

As is the case for many tropical insects, few data are available on the natural history of *E. hegesia*. In this paper, therefore, we present the results of the first comprehensive study of the ecology and life history of this species. These data provide necessary background information as a prelude to more detailed investigations of chemical mediation of the interaction between the hostplant and this butterfly. Specifically, our objectives are to: (1) provide detailed observations of the life cycle of *E. hegesia* using captive-reared individuals, providing methods for captive rearing; (2) compare the lifespan and size of individuals in captivity and the field; (3) examine the age-structure, size and sex ratio of populations in nature; (4) examine the distribution of larvae on hostplants; (5) compare relative survival and performance of larvae on commonly used hostplants; (6) assess the degree of butterfly movement between hostplant populations; and (7) provide information on the level and kinds of mortality sources experienced by adult butterflies.

MATERIALS AND METHODS

Study organisms. There are two extant species in the genus *Euptoieta*. *Euptoieta hegesia* Cramer is limited in its distribution to Mexico and Central America south to Colombia in South America and to the islands of the Caribbean (Brown & Heineman 1972, DeVries 1987, Smith et al. 1994). *Euptoieta claudia* Cramer has a similar but broader distribution that extends both further north and south of the range of *E. hegesia*. There is some debate as to whether additional taxa, including *E. hortensia* Blanchard (Brown & Heineman 1972, A. Shapiro, pers. comm.), and *E. bogotana* Staudinger (DeVries 1987; possibly a high Andean race of *E. claudia*, K. Brown Jr., pers. comm.), warrant recognition as distinct species. *Euptoieta* is generally placed in the subfamily Argynninae, allied with both the North American and Old World argynnines and the Neotropical Heliconiinae (Dos Passos & Grey 1945, Clark 1947, Ehrlich 1958). Scott (1985) suggested that *Euptoieta* shares many ancestral traits with these two lineages, noting that the wing venation of *Euptoieta* is almost identical to that of *Agraulis vanillae* L., a heliconiid with a number of primitive characteristics. This classification is supported by more recent analyses (Ackery 1988, Harvey 1991, Martin & Pashley 1992). Recent molecular work by Weller et al. (1996) and A. Brower (pers. comm.) suggests that the Argynninae, Heliconiinae and Acraeinae form a monophyletic clade.

Turnera ulmifolia is the primary larval hostplant of *E. hegesia* on Jamaica (see below, Brown & Heineman 1972). *Euptoieta hegesia* is also known to use other *Turnera* species and varieties including *T. scabra* Mills. in the Dominican Republic (JSS, pers. obs.), *T. ulmifolia* (probably *T. subulata* Smith) in Brazil (K. Brown Jr., pers. comm.) and Colombia (Hallman 1979) as well as cyanogenic *Passiflora* species, particularly *P. suberosa* L. and *P. foetida* L. on Jamaica (T. Turner, pers. comm., PJS, pers. obs.) and *P. foetida* in Costa Rica (Smiley 1983). *Euptoieta claudia* is also found on Jamaica (but is confined to a region of the Blue Mountains above 1220 m) where it feeds on *Viola patrinii* DC., an acyanogenic plant (PJS, pers. obs. and unpubl. data, T. Turner, pers. comm., Smith et al. 1994).

While no detailed work exists on the life history and ecology of *E. hegesia*, most of the available information is attributable to the work of Tom Turner (*in* Brown & Heineman 1972, Smith et al. 1994). Turner indicates that eggs are laid on the upper or terminal leaves of hostplants in the wild, that the egg stage lasts five days, that larvae develop over 9–12 days and that pupae develop over eight days. These data yield a published egg to adult (i.e., generation) time of 22–25 days. Larvae are brick red with black spines until their third instar when the ground colour deepens to maroon and a silver/white dorsal line edged with black and two similar lateral lines appear—suggesting that larvae are aposematically colored. Pupae vary from tan to black (pers. obs.) with silver and gold markings. Adults are "medium-size orange-tawny butterflies" (Brown & Heineman 1972:210) with extensive black markings on the upperside (similar to *A. vanillae* but lacking the elongated forewings) and with the undersides mottled brown and purple. Published, mostly anecdotal, accounts of various aspects of the anatomy, life cycle and hostplant use of *E. hegesia*, with particular reference to Jamaica, include Swainson (1901), Longstaff (1908), Kaye (1926), Brown and Heineman (1972) and Smith et al. (1994). Further accounts are found in Scudder (1889), D'Almeida (1923), Ross (1964) and DeVries (1987).

Turnera ulmifolia L. is a weedy shrub common to roadsides and coastal scrub habitats throughout the Neotropics (Barrett 1978, Barrett & Shore 1987). It is a perennial that produces many ephemeral (<1 day) flowers and is known to show a wide range of morphological and reproductive variation on Jamaica (duQuesnay 1971, Barrett & Shore 1987). Plant populations are generally discrete, often small and widely separated, with potentially little gene flow among populations (Barrett 1978, Belaoussoff & Shore 1995). Shore and Obrist (1992) documented extensive variation for cyanogenesis across a number of species, taxonomic varieties and populations of *Turnera*. There is a wide range of cyanogenesis in *T. ulmifolia* from Jamaica (Schappert & Shore 1995). The presence of cyanogenic glycosides with a cyclopentenoid structure, in addition to morphological, embryological, and DNA sequence data, ally the Turneraceae with the Passifloraceae and other members of the order Violales (Vijayaraghavan & Kaur 1966, Cronquist 1981, Spencer et al. 1985, Spencer 1988, Chase & Swenson 1995). Interestingly, the patterns of host use by related species of butterflies led Ehrlich and Raven (1964:594–595) to "confidently predict" that the biochemical basis for the association of these plant families would eventually be found.

Rearing in captivity. To investigate the life cycle and conduct laboratory experiments, larvae were reared on potted plants of *T. ulmifolia* on which eggs had been laid. When larvae began wandering in later instars, or if individual rearing was needed, they were transferred to rearing cups. Rearing cups consisted of 260 ml disposable plastic cups with an inner circle, approximately 42 mm in diameter, cut out of the transparent lid. A 30 ml cup with a small hole punched in its lid was filled with water, capped, a small shoot of hostplant inserted and was placed in the bottom of the larger cup. A 100 mm × 100 mm square of bridal veiling was sandwiched between the cup and the transparent lid to prevent larvae from escaping, and allow sufficient air movement to prevent the build-up of fungus. The netting also provided a preferred pupation site for this species. Single larvae kept in cups generally needed cleaning and replenishing of the hostplant every 2–5 days. Groups of similar sized larvae were reared on potted plants in large (10–12 L) plastic pails with veil tops secured by an elastic. All rearing was conducted in the glasshouse at York University in Toronto, Ontario, Canada under natural summer photoperiod conditions.

This method of individual rearing provides a good balance between space requirements, labour intensiveness and the maintenance of reasonably sanitary conditions because cups can be contained in plant trays to allow easy movement and to allow visual checks for food and cleanliness in a timely manner. Cleaning and re-feeding were quickly accomplished by removing the larvae and old inner cup, wiping, inserting a new inner cup with fresh foodplant, and reintroducing the larvae. The pupae were easily removed from the bridal veiling with their silk pads intact. The pads were sandwiched between two pieces of marking tape and hung on the side walls of rearing cages with wire paper clips. Adults were housed in cages and mating and oviposition occur even in very small cages (30 cm × 30 cm × 30 cm). However, we commonly used 64 cm × 71 cm × 85 cm high wooden frame cages with wire screen floors and covered in bridal veiling for the maintenance and breeding of adults. Sex ratio in the cages can be maintained by monitoring the sex of pu-

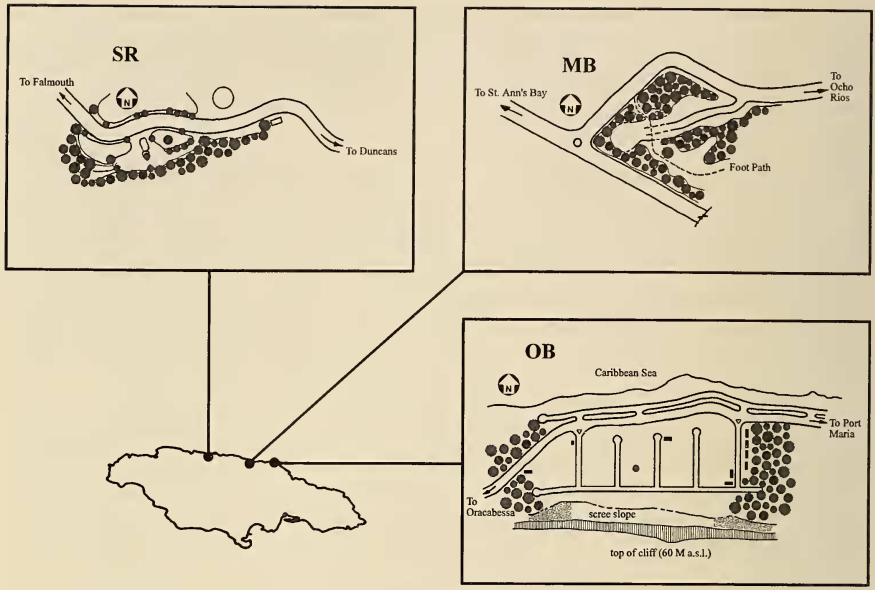

FIG. 1. Location and site plans for three *T. ulmifolia/E. hegesia* populations studied on Jamaica. Not to scale.

pae (determined by pupal mass—females are significantly larger than males, see below and Table 1). Mating of females as they eclose is common.

Adults were fed daily with a honey water/salts/amino acid supplement (Lederhouse et al. 1990) placed in *T. ulmifolia* flowers on oviposition plants and in individual flowers inverted on the top of the cage. In addition, *Lantana* spp. (Verbenaceae), *Pentas* sp. (Rubiaceae) and *Ageratum* sp. (Compositae) are provided as nectar sources in the cages. Some individual butterflies (e.g., ovipositing females) were fed manually by uncoiling their proboscis into nectar supplement contained in *T. ulmifolia* flowers on the cage bottom. Recently we have begun using a long-lived artificial nectar, modified from Lederhouse et al. (1990) and O. R. Taylor (pers. comm., for captive rearing of Monarchs), presented to butterflies in shallow cups clipped to the corner posts of the cages approx. 20 cm from the top of the cage. The nectar is resistant to fermentation and can be left for up to three weeks with daily additions of distilled water to offset evaporation. It has proven to be very attractive to the butterflies and has greatly reduced manual feeding requirements of females. Our recipe for artificial nectar is as follows: to 1 L of distilled water, add 150 g high-grade natural honey (or sugar); 4 g ascorbic acid (vitamin C); 2 g 2,4-hexanedienoic acid (sorbic acid); 2 g p-hydroxybenzoic acid methyl ester (methylparaben or Tegosept©); 5 g bovine casein, acid hydrolysate; 7.2 g Potassium chloride (KCl); 0.24 g Calcium chloride ($CaCl_2$); and 0.10 g Sodium chloride (NaCl).

Performance of larvae on hostplants. We conducted experiments to assess the performance of larvae on the three most commonly used Jamaican hostplants: *T. ulmifolia*, *P. foetida* and *P. suberosa*. A sample of fresh-hatched larvae (total 72) was selected from four *T. ulmifolia* oviposition plants that had each been available to at least five ovipositing females (reared on *T. ulmifolia*) in each of four cages for four hours. The larvae, therefore, were even-aged and likely represented the progeny of at least 20 matings. The larvae were reared in groups of 12 in six rearing buckets containing abundant, mature, flowering hostplants: two with potted plants of *P. foetida*, two with *P. suberosa* and two with *T. ulmifolia*. The presence/absence of larvae was monitored every 2–3 days. We

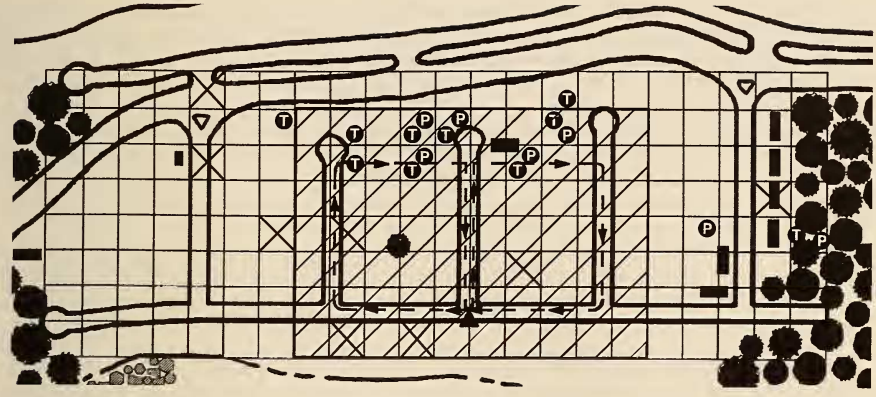

FIG. 2. Site plan of OB showing location and approximate effective area of the *E. hegesia* population studied (crosshatched), the length and direction of the survey transect used in the MRR study (dotted line), and the location of the hostplants found and quadrats surveyed during the hostplant survey. T = *T. ulmifolia*, P = *Passiflora* spp., X through quadrat denotes a surveyed quadrat where no hostplants were found. Each quadrat is 30.5 m square.

recorded the date of pupation and the mass of the pupa the following day. The entire experiment was replicated in the subsequent generation, again with larvae from eggs laid by *T. ulmifolia*-reared adults.

Study sites and distribution of *E. hegesia* on Jamaica. A survey of numbers of potential hostplants was conducted at one large (OB, near Oracabessa, St. Mary, >20 ha) and two small (MB, near Mammee Bay, St. Ann, & SR, near Duncans, Trelawny, <2 ha each) *T. ulmifolia* populations on the north coast of Jamaica in June to August of 1991 (Fig. 1). A survey was conducted at OB in August by mapping and dividing the site into 176 contiguous 30.5 × 30.5 m quadrats (Fig. 2), counting all plants of *T. ulmifolia* encountered, and recording the presence/absence of *Passiflora* species in 20 randomly selected quadrats. A complete count of all of the available hostplants was made at the two small populations (MB & SR) in late-June and again in August. On the final visits to each site, the numbers and distributions of eggs and larvae found on *T. ulmifolia* were recorded (an exhaustive search was carried out at MB and SR and a random sample of 100 plants was examined at OB and at another large site 1 km east of OB). The distributions of eggs and larvae on plants was also recorded at MB and SR in June and December of 1992 and at an inland site, EW (near Ewarton, St. Catherine), in June 1991 and June 1992.

To determine the distribution of *E. hegesia* on the island of Jamaica, the presence of larvae and adults was recorded at more than forty *T. ulmifolia* populations from around the island that were systematically surveyed in June of 1990 and June to August of 1991. Additional data on presence of larvae in a number of plant populations were recorded in January of 1989 by JSS, and for adults and larvae in June and December of 1992 and June and December of 1995 by PJS.

Butterfly population and damage surveys. We conducted a mark-release-recapture (MRR) study of *E. hegesia*, using Bailey's Triple Catch design (Bailey 1952), in the large (OB) and both small (MB & SR) *T. ulmifolia* populations in June of 1991, with continued study in the large population through July and August of 1991 (see Fig. 1 for site maps). A transect slightly more than 1 km in length through representative habitat (6.5 ha, approx. 35% of the habitat) was followed at OB (Fig. 2). At MB, a relatively flat and wind-protected glade surrounded by trees, we traversed the length of the access road plus the foot path. At the SR site, we wandered haphazardly throughout the uneven terrain in the

area. The OB site, described as "raised coral beach" by Asprey and Loveless (1958), is bounded by the sea to the north and a cliff-face to the south with secondary forest bounding the east and west. A large plant population located 1 km east of OB and separated from the MRR site by second growth forest was monitored in August for butterflies marked at the OB site, to assess interpopulation movement over relatively short distances.

On the first three visits to each site (and each month at OB) all captures were carefully marked on the underside of the left hindwing using an indelible fine point marker to show the mark day and a unique individual number. A different marker color was used for each of the three mark occasions. For each initial capture we recorded sex, size (maximum length of forewing), a qualitative estimate of age (wear, as loss of scales, in 5 classes: very fresh, fresh, medium, worn, very worn), and wing damage recorded for each wing (left, right, fore, or hind), damage location (tip, outer margin, trailing edge), type (tear, notch, frayed), and whether damage was symmetrical (i.e., mirror image) or asymmetrical between adjacent wing pairs. As many butterflies as could be captured at each site were carefully netted. Capture effort was standardized by time: short visits of 1 h sufficed at MB & SR while 3.5–4 h were required to traverse the transect on each occasion at OB. Captures commenced at 0830 h at OB and SR and at 1300 h at MB. All marking, age estimation and categorization of damage was done by PJS.

Marking visits to the sites were spaced 2–3 days apart to minimize the effects of handling on butterflies and to ensure that marked butterflies mixed with the unmarked population (Morton 1982, Gall 1985, Mallet et al. 1987, Orive & Baughman 1989). Subsequent visits, 3–7 days apart, were made to obtain data on the lifespan of adult butterflies. Mark visits in 1991 were conducted on 7, 9, and 11 June at OB and MB and 8, 10 and 12 June at SR. A total of six visits was made to each site over 16 days. At OB, mark visits only were made on 6, 8 and 10 July while mark visits in August were conducted on 4, 7, 10 and 13 August with one subsequent visit on 21 August. A fourth mark occasion was necessary in August due to the interruption of the first visit by inclement weather. There were 29 days between the onset of marking in June and July and between July and August at OB, roughly corresponding to the generation time in captivity (see below). On subsequent visits, only the number of unmarked butterflies and the identity and number of recaptures was recorded. Change in condition and new damage sustained by previously undamaged butterflies was recorded for a subsample of individual recaptures (n = 26) made at OB in June.

The frequency and type of wing damage sustained by *E. hegesia* during this population study was compared to a previous collection of a series of 30 specimens and a subsequent collection of a series of 25 specimens, taken from the OB site in June of 1990 and June of 1995, respectively. At the latter time we also collected a short series of 12 specimens each of 2 species which co-occur at the OB site—the close relative *Agraulis vanillae* L. (Heliconiinae) and more distantly related *Anartia jatrophe* Möschler (Nymphalinae)—to assess whether *E. hegesia* is unusual in the frequency of wing damage. A series of 25 specimens of the sister taxon, *E. claudia*, taken below Cinchona Gardens in the Blue Mountains (approx. 1300 m) in August 1991 was also examined for frequency and type of damage. All of these species are of similar size and are remarkably alike in their adult behaviour.

Data analysis. Population and lifespan (i.e., residence time) estimates including estimates for subsets of the data by sex, as well as tests of MRR assumptions, including equal catchability, and absence of marking and handling effects, were calculated using the PC program CAPTABLE (Arndt & Arnold 1994). Since *a priori* evidence was not available, and because one of our objectives was to assess interpopulation movements, population estimates were calculated for both open and closed population models to avoid potential bias due to application of the incorrect model (open model: Bailey's Triple Catch, Bailey 1952—a special case of the Fisher-Ford model, Gall 1985; closed model: Lincoln-Peterson, Begon 1979). Lifespan estimates were calculated using Scott's Method I, based on Jolly-Seber population estimates, which provides a single minimum daily survival rate for the duration of each study at each site and month (Scott 1973).

Total damage scores were assigned by summing the presence of damage for each wing (minimum score = 0, maximum = 4). For subjects with damage, total symmetry was calculated similarly (minimum score = 0, maximum = 2). Statistical analyses including t-tests and analyses of variance (ANOVA) were conducted using SAS (1988) unless otherwise in-

dicated. Homogeneity of variance assumptions were tested; where the assumptions failed, t-tests were performed using Satterthwaite's approximation (SAS 1988). Tests of independence and correlation analyses were conducted using Minitab (1994) Release 10. Where comparisons involved the ranked age data, Mann-Whitney or Kruskal-Wallis tests were used, and we used Spearman's rank correlation (r_s) to examine the relationship between age and size. Distributions of eggs and larvae on plants were tested against Poisson and negative binomial distributions following Ludwig and Reynolds (1988).

RESULTS

Life history of *E. hegesia* in captivity. Our laboratory rearing methods proved to be quite successful, as numerous butterfly progeny could be raised fairly readily. The major limiting factor in rearing is the number of host plants that can be grown to feed the larvae. Typical results of lab rearing, from June of 1990, are as follows: a total of 212 *E. hegesia* larvae and pupae, in varying numbers, were collected from 10 sites in Jamaica and brought back to our glasshouse facilities in Toronto; approximately 75% of the sample pupated and eclosed normally yielding 156 adults; in the first lab-reared generation we obtained 4189 eggs from 21 crosses (approximately 200 eggs/mating) yielding a total of approximately 3800 larvae. Captive populations are easily maintained.

It is intriguing to note that in the years 1990 through 1992 we collected and reared 136 wild-collected eggs and 973 wild larvae of all stages, with a number of pupations having occurred in the field prior to our return, and have never found a parasitoid. Larvae that died and eggs or pupae that failed to eclose were monitored for up to two weeks without encountering parasitoids. None of the more than 1375 eggs, larvae and pupae that we have collected in the wild over a six year period has yielded a parasitoid.

In captivity, the life history of *E. hegesia* encompasses approximately five days in the egg stage (mean ± SD: 4.97 ± 0.38 days, n = 907 eggs), with the larvae progressing through five instars in 12–15 days (13.8 ± 1.5 days, n = 112), and the pupal period lasting 8–9 days (8.5 ± 0.8 days, n = 112). Eggs are laid singly, predominately on the underside of terminal leaves on *T. ulmifolia* (but not exclusively so), and average 0.183 ± 0.013 mg each (n = 43 groups containing a total of 3311 eggs). Full sib progeny show a 1:1 sex ratio with peak male eclosion occurring approximately two days before females and the number of days from egg hatch to eclosion being one day longer, on average, for females (Table 1). Female butterflies are immediately receptive to mating upon eclosion—time from eclosion to mating is significantly shorter for females (Table 1), however, oviposition has not been recorded on the day of eclosion. Overall, *E. hegesia* has a 28–30 day egg-to-egg cycle in captivity and may prove to be a useful species for genetic studies as a result of its short generation time and high fecundity.

TABLE 1. Sexually dimorphic characters in captive-reared and wild *E. hegesia* from Jamaica. A Kruskal-Wallis test was used for Field age class and the statistic shown is a chi-square approximation; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

		Males			Females			
	Character	N	mean	(SD)	N	mean	(SD)	t
Lab	adult size (mass at eclosion, mg)	190	111.1	(38.9)	220	145.5	(49.1)	7.78 ***
	mass at pupation (mg)	56	260.0	(26.0)	39	311.1	(27.2)	9.18 ***
	total development time (days)	56	26.9	(1.4)	39	27.6	(1.2)	2.43 *
	larval development time (days)	56	13.5	(1.4)	39	14.2	(1.3)	2.47 *
	pupation period (days)	56	8.5	(0.5)	39	8.4	(0.6)	0.48
	eclosion to mating time (days)	24	1.7	(1.5)	22	0.8	(1.0)	2.37 *
	adult lifespan (days)	123	6.8	(4.0)	103	6.5	(3.2)	0.75
Field	adult size (wing length, mm)	267	27.2	(1.2)	208	29.4	(1.5)	17.45 ***
	age class (wing wear class)	272	2.50	(1.16)	211	2.52	(1.15)	0.09
	total damage	272	0.54	(.92)	210	0.78	(1.04)	2.59 *
	damage frequency	272	0.34	(.47)	210	0.46	(.50)	2.75 **
	age at subsequent damage (days)	5	5.8	(1.6)	8	3.5	(.3)	3.00 *
	total symmetrical damage	272	0.06	(.25)	210	0.12	(.34)	2.16 *
	symmetrical damage frequency	91	0.17	(.37)	96	0.25	(.44)	1.43

TABLE 2. Survivorship and relative performance of captive-reared *E. hegesia* on the three most commonly used hostplants on Jamaica. Means with the same letter are not significantly different at $p < 0.05$, SNK test following one-way ANOVA.

Hostplant	Generation	N	Survival to			Mean mass (SE) at pupation (g)	Mean time (SE) to pupation
			3rd instar	pupation	eclosion		
T. ulmifolia	1	24	100	100	—	0.253 (0.009)[a]	11.8 (0.21)[a]
P. suberosa		24	96	42	—	0.281 (0.013)[ab]	16.3 (0.34)[b]
P. foetida		24	58	46	—	0.336 (0.016)[b]	15.0 (0.54)[b]
T. ulmifolia	2	24	100	100	75	0.264 (0.010)[a]	13.4 (0.25)[a]
P. suberosa		24	100	92	67	0.291 (0.008)[ab]	18.0 (0.50)[b]
P. foetida		24	83	79	54	0.306 (0.010)[b]	15.5 (0.34)[c]

There is considerable dimorphism between the sexes. Females are significantly larger than males both in nature (wing length; Table 1) and in captivity (fresh adult mass and pupal mass; Table 1). Size dimorphism may be related to the increased time required for larval development in females—females take significantly longer to develop from date of oviposition through to eclosure (total development time; Table 1), largely as a result of increased larval development time since pupation periods do not differ between the sexes (Table 1). Captive females lay an average of 27 eggs per day (27 ± 11.2, n = 14 females over 4 consecutive days) and lifespan in captivity does not differ between sexes (Table 1).

Performance of larvae on hostplants. There is some ambiguity in the literature about whether *T. ulmifolia* or a species of *Passiflora* is the primary hostplant of *E. hegesia*. Turner has commented that "the larva takes the longer time to mature when fed on *Turnera*" (Brown & Heineman 1972:210). To address this issue we conducted experiments to assess the performance of larvae on the three most commonly used Jamaican hostplants: *T. ulmifolia*, *P. foetida* and *P. suberosa*. Larvae reared on *T. ulmifolia* had the highest survivorship and a significantly faster development time but had the lowest pupation mass (Table 2). Larvae had lower survivorship on both species of *Passiflora*. Larvae reared on *P. foetida* had an intermediate development time and highest pupation mass whereas those reared on *P. suberosa* had the longest development time and median pupation mass. Two consecutive generations exhibited identical patterns (Table 2). Interestingly, mortality of larvae on *P. foetida* was in early instars, possibly due to the extensive glandular trichomes of this species, whereas mortality of larvae on *P. suberosa* occurred in later instars. All larvae reared on *T. ulmifolia* survived to pupation. Eclosion success in the second generation was lowest for *P. foetida* and highest for *T. ulmifolia*. These data suggest that overall host plant suitability for Jamaican *E. hegesia* is *T. ulmifolia* > *P. suberosa* > *P. foetida*.

FIG. 3. Distibution of *E. hegesia* larvae and adults encountered on Jamaica from 1989 through 1995. Open symbols denote larvae, closed symbols adults. Study sites mentioned in the text are denoted by two-letter codes.

Distribution of *E. hegesia* on Jamaica. Larvae and adults of *E. hegesia* have been found at many *T. ulmifolia* populations; however, their abundances vary greatly. Our findings suggest that *E. hegesia* is more common in the largely acyanogenic hostplant populations on the north coast at least during the summer months (see Fig. 3, and Schappert & Shore 1995). Observations from the winter of 1989, 1992 and 1995 indicated the presence of larvae at highly cyanogenic southern populations more commonly than do all of our summer records.

Hostplant population size and distribution of larvae on hosts. The hostplant survey at OB (Fig. 2) yielded 311 *T. ulmifolia* plants in 11 (55%) of the 20 quadrats. Multiplying the 176 total quadrats by the mean number of *T. ulmifolia* in the surveyed quadrats (15.6, range: 0–82) yields an estimate of more than 2700 plants at this site. Four species of *Passiflora* were found in 7 quadrats (35%) but the percentage of quadrats occupied by the species varied (*P. suberosa,* 25%; *P. perfoliata* L., 20%; *P. rubra* L., 15%; *P. foetida,* 10%). *Turnera ulmifolia* and *Passiflora* spp. were commonly found in the same quadrat (Fig. 2). Repeated surveys of all available *T. ulmifolia* hostplants during 1991 and 1992 at the two small study sites revealed that the MB site fluctuated between 14 and 30 plants while SR varied from 18 to 47 plants. We did not find any species of *Passiflora* at either site.

The results of surveys for numbers of eggs and larvae on plants at the three main study sites (OB, MB & SR), the site immediately east of OB and a fifth site near Ewarton in the center of the island, conducted in 1991 and 1992, are presented in Table 3. The distribution of larvae on plants is non-random (8 of 11 larval distributions are significantly different from Poisson) and clumped (9 of 11 are not significantly different from negative binomial). A count of larvae on one of two large *P. foetida*

TABLE 3. Distribution of larvae of *E. hegesia* on *T. ulmifolia* and chi-square goodness of fit tests against random (Poisson) and clumped (negative binomial) distributions in five *T. ulmifolia* populations on Jamaica. 1992a = early June, 1992b = late June, 1992W = Dec. Asterisks indicate significant departure from listed distribution at $p < 0.05$.

Site	Year	Tot. no. plants	Tot. no. larvae	Number of plants with 0, 1, 2 . . . larvae											Mean (SD) larvae per plant	Poisson χ^2 (df)	NegBinom χ^2 (df)
				0	1	2	3	4	5	6	7	8	9	>9			
EW	1991	51	25	39	7	2	1	1	0	0	1	0	0	0	0.49 (1.24)	6.5 (1)*	0.2 (1)
	1992	38	50	21	7	2	3	2	0	1	1	0	1	0	1.32 (2.17)	20.9 (2)*	0.9 (1)
MB	1991	20	16	14	2	1	2	0	0	1	0	0	0	0	0.80 (1.58)	6.6 (1)*	0.6 (1)
	1992a	14	13	9	3	0	0	0	2	0	0	0	0	0	0.93 (1.77)	3.6 (1)	1.4 (1)
	1992b	16	22	11	3	0	0	0	0	1	0	0	0	1	1.38 (3.44)	16.2 (1)*	2.0 (1)
	1992W	30	21	18	6	3	3	0	0	0	0	0	0	0	0.70 (1.02)	2.9 (1)	0.4 (1)
OBW	1991	100	121	82	4	4	1	1	2	2	0	0	0	4	1.19 (4.79)	134.8 (2)*	1.0 (1)
OBE	1991	100	68	78	1	10	7	2	0	0	0	0	2	0	0.68 (1.59)	66.8 (2)*	15.4 (1)*
SR	1991	18	39	7	5	1	1	0	2	0	1	0	0	1	2.17 (3.22)	8.0 (1)*	1.4 (1)
	1992	47	69	25	9	2	4	0	1	4	1	1	0	0	1.47 (2.25)	30.2 (2)*	1.8 (1)
	1992W	24	54	11	0	3	4	0	4	0	0	2	0	0	2.25 (2.59)	2.8 (1)	5.7 (1)*

TABLE 4. Species and flower color of nectar sources used by *E. hegesia* on Jamaica.

Taxon	Flower color
Acanthaceae	
Blechum pyramidatum (Lam.) Urb.	lilac/blue
Asclepiadaceae	
Asclepias curassavica L.	red/orange
Boraginaceae	
Heliotropium indicum L.	white
Compositae	
Ageratum houstonianum Mill.	blue
Bidens pilosa L.	white/yellow
Bidens reptans (L.) G. Don	yellow
Borrichia arborescens (L.) DC.	yellow
Eupatorium odoratum L.	pink/blue
Spilanthes urens Jacq.	white
Wedelia trilobata (L.) Hitchc.	yellow
Rubiaceae	
Borreria laevis (Lam.) Griseb.	white/pink
Sterculiaceae	
Melochia tomentosa L.	white/pink
Turneraceae	
Turnera ulmifolia L.	yellow
Verbenaceae	
Lantana camera L.	yellow/orange
Stachytarpheta jamaicensis (L.) Vahl	blue

plants at OB yielded four *E. hegesia* and eight *A. vanillae* larvae. Larvae were not seen on a number of other *P. suberosa* and *P. foetida* that were surveyed; however, *E. hegesia* females have been observed to oviposit on all of the species of *Passiflora* found at the OB site. The vast majority of the ovipositions we observed occurred on *T. ulmifolia*.

Butterfly behavior and population structure. Our observations of adult *E. hegesia* revealed very fast, straight-line flights from shortly after dawn until about 8 am. At about this time flight behavior changes remarkably and becomes characterized by relatively slow, wandering flights within 30–45 cm of the ground. Butterflies stop frequently to rest or to nectar at many low herbs and shrubs, which are also commonly used by other butterflies. The flowering species visited span several plant families that exhibit a wide range of flower color and morphology (Table 4). Flowers of *T. ulmifolia*, used by a variety of other nectaring butterflies, were not commonly used by *E. hegesia*. Resting behavior also changes during the day from open-wing "basking" early in the day to folded-wing stances later in the day. Males appear to spend more time in flight, presumably patrolling in search of mates, and they inter-

TABLE 5. Common butterfly species found in typical *T. ulmifolia/E. hegesia* habitat on Jamaica.

Papilionidae
Battus polydamas Rothschild & Jordan
Papilio andraemon Hübner
Pieridae
Ascia monuste Godart
Eurema lisa (Ménétriés)
Lycaenidae
Strymon acis (Comstock & Huntington)
Hemiargus hanno (Fabricius)
Nymphalidae
Anartia jatrophe Möschler
Junonia evarete Felder & Felder
Danaus gilippus (H. W. Bates)
Phyciodes frisia Poey
Mestra dorcas Fabricius
Agraulis vanillae L.
Hesperiidae
Urbanus proteus (L.)
Polygonus leo Evans
Pyrgus oileus (L.)

act frequently with other males, females and a variety of other butterfly species, most notably the similarly sized and coloured *Agraulis vanillae*. Other butterfly species common in the habitats in which *E. hegesia* and *T. ulmifolia* are found are listed in Table 5.

We netted a total of 730 individuals with 483 (66%) being marked during the first three visits to each of the three sites over the length of the study. Most of the captures (622) and 427 of the marked individuals (68%) were from the large hostplant population (OB). No marked butterflies were recaptured at the site 1 km east of OB. The proportion of marked butterflies recaptured on subsequent visits was generally high (range 10–23%, up to 11 days after the initial visit) and the maximum length of time elapsed between marking and last recapture for any particular individual (i.e., the minimum age of those individuals) was 14 days. Population size estimates, whether from closed (Lincoln-Peterson) or open (Bailey's Triple Catch) population models, were very similar. Table 6 provides estimates of the total population sizes derived using the two methods as well as separate estimates of the numbers of males and females at MB and for the months of June and August at OB. Observed sex ratios, daily survival rates, expected residence times (i.e., estimated lifespan), and maximum observed lifespans are also presented in Table 6.

Tests of the assumptions made in MRR studies—including lack of marking effects, equal catchability of sexes, independence of recapture

TABLE 6. Population size estimates (second visit), observed sex ratio, survival rates and expected lifespan (residency) and maximum observed lifespan of *E. hegesia* at three sites on Jamaica. BTC = Bailey's Triple Catch, L-P = Lincoln-Peterson, Expected lifespan calculated using Scott's Method I (Scott 1973).

			Estimation Method							
			BTC		L-P			B.T.C. survival		
Site	Month	Captures included	N	(SE)	N	(SE)	Observed sex ratio (% males)	s	(SE)	Expected lifespan (residence time)	Maximum observed lifespan
OB	June	all	233	(75)	282	(82)	82	0.81	(0.21)	5.6	14
		males	131	(57)	176	(72)		0.73	(0.26)	7.2	14
		females	78	(36)	88	(40)		0.86	(0.32)	2.4	9
	July	all	474	(346)	247	(101)	55	0.17		2.1	5
	August	all	540	(596)	517	(164)	63	0.78	(0.71)	3.9	12
		males	343		315	(157)		0.56	(0.77)	5.8	12
		females	121	(183)	178	(80)		0.76	(1.10)	10.6	7
MB	June	all	22.5	(11.7)	24.3	(9.2)	57	1.29	(0.45)	8.5	12
		males	14.5	(7.6)	15.0	(6.2)		1.24	(0.29)	7.1	12
		females	12.0	(13.4)	7.0	(9.3)		0.81		11.7	12
SR	June	all	12.5		25.7	(12.8)	78	0.46		3.6	9

from previous capture, and assumptions of constant survival or residency (Begon 1979, Tabashnik 1980, Gall 1985, Arndt & Arnold 1994)—revealed that there was no increase in mortality due to marking and no dependence of the probability of recapture based on previous capture (all marks had equal probability of recapture) for all sites and all months at OB. There was also no significant difference between male and female catchability for the three sites or the three months at OB. Females were significantly more likely to die or emigrate from OB in June ($F_{1,3} = 12.1$, $p < 0.05$, M:F ratio = 1.234) but there was no significant difference in joint residency in July or August or at the small sites. This finding is supported by the low residence time (expected lifespan) for females in June at OB in comparison to males (see Table 6). There is an overall sex ratio bias towards males at all sites for all months, a common finding in MRR studies of butterflies (Gall 1985); however, the proportion of recaptures to captures did not differ between sexes (as expected from results of the equal catchability tests).

Females were significantly larger than males over all sites (Table 1) with the smallest butterflies found at MB ($F_{2,472} = 6.98$, $p < 0.001$, MB = SR & SR = OB, SNK multiple comparisons test). Sexes did not differ in median age (based on wing wear scores, Kruskal-Wallis test, see Table 1); however, a marginal but non-significant difference was found between sites ($F_{2,480} = 2.60$, $p > 0.10$). Older butterflies (i.e., worn and very worn classes) were, on average, significantly smaller than younger butterflies ($F_{4,470} = 4.10$, $p < 0.01$). This variation was more pronounced in males ($F_{4,267} = 5.37$, $p < 0.001$) than in females ($F_{4,208} = 2.51$, $p < 0.05$). The frequency of butterflies in the five age classes at the OB population was similar for all three months (Fig. 4). More than 82% of the butterflies were, on average, less than medium worn (middle-aged). The SR site had proportionately more very fresh (VF) individuals, with greater than 90% of all butterflies being less than medium worn. The MB site had fewer medium worn and a greater percentage of very worn (VW) individuals with only 70% of butterflies less than medium worn (Fig. 4).

Wing damage sustained by butterflies. Thirty-eight percent of all captures exhibited some wing damage at their initial capture and the sex ratio of captures with damage approached unity (0.95 males to each female) despite the overall male-biased sex ratio of all captures (1.3 males to each female). Females were damaged more frequently (46% of females vs. 33% of males, $\chi^2 = 3.84$, $p = 0.05$) and sustained significantly more total damage than males (Table 1) but differences were not significant between sites, and no significant differences were found between months at OB, for either sex. Damaged individuals were consistently assigned to older age-classes, based upon wing wear. A positive correlation

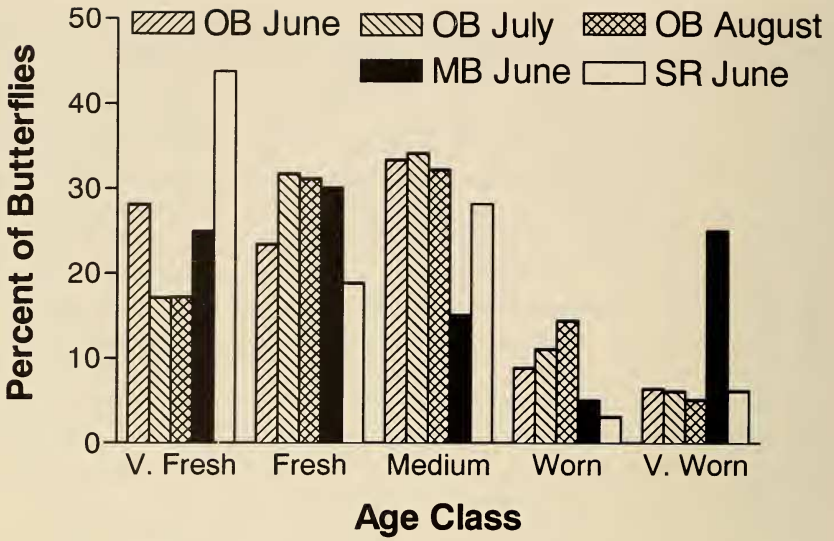

FIG. 4. Comparison of butterfly age structure at one large (OB) and two small (MB & SR) *T. ulmifolia/E. hegesia* populations on Jamaica.

between total damage and age explains 36% of the variation ($r_s = 0.63$, $p < 0.001$). Males that were not damaged at their initial capture attained a significantly greater maximum age than those that were damaged at first capture ($F_{1, 270} = 5.30$, $p < 0.05$) and previously undamaged males were recaptured more often than those that were damaged at their initial capture ($F_{1, 270} = 7.37$, $p < 0.01$); however, neither of these was true for females.

Comparison of the frequency, location and type of damage (forewing tip and margin, forewing notch, hindwing margin, hindwing notch) in symmetrical and asymmetrical classes against the capture sex ratio revealed no significant association for any combination except for a significant deviation in the frequency of asymmetric hindwing notches ($\chi^2 = 7.3$, $p < 0.01$, with females receiving disproportionately greater damage). Females had a greater frequency of symmetrical damage (28 vs. 13 males), which is significantly different from the capture sex ratio ($\chi^2 = 9.1$, $p < 0.01$) but not from an expectation of an equal sex ratio. New damage was recorded on second captures for 5 males and 8 females of 26 individuals examined. Comparison of the age (i.e., wing wear) at recapture revealed that females were significantly younger when damage occurred (Table 1).

The 38% of all initial captures from the MRR study, over all months and sites, that exhibited some damage is remarkably similar to the proportion of damaged specimens collected in 1990 and for the three spe-

TABLE 7. Sex ratio and damage frequency in four species of Jamaican butterflies. *E. hegesia, A. vanillae* and *A. jatrophe* are sympatric in lowland coastal habitats while *E. claudia* occurs in the Blue Mountains above 1220 m.

Species	Year	Total no. of captures	Damage freq. (% of captures)	Sex ratio (% males)	Damage freq. (% males)
E. hegesia	1990	30	33	63	70
	1991	483	38	55–82	48
	1995	25	32	64	63
A. vanillae	1995	12	42	67	75
A. jatrophe	1995	12	33	83	100
E. claudia	1991	25	12	52	100

cies taken at the OB site in June of 1995 (Table 7). One of the 1990 *E. hegesia* specimens shows evidence (asymmetric hindwing damage) of an attack by a bird (see Fig. 5), one had symmetrical hindwing damage, and six specimens had asymmetrical hindwing damage. One of the 8 damaged *E. hegesia* in the 1995 sample showed evidence of symmetrical hindwing damage (see Fig. 5), one had only forewing damage whereas the remaining six had asymmetrical damage to the hindwings. All of the *Anartia jatrophe* that were damaged had asymmetrical hindwing damage whereas only one half of the damaged *Agraulis vanillae* showed hindwing damage. In comparison, damaged individuals were very infrequent (Table 7) in the sample of *E. claudia* taken in the Blue Mountains in August of 1991 and none of the 3 damaged specimens had hindwing damage.

DISCUSSION

Most studies of the population structure and dynamics of tropical insects have concentrated on rainforest species (Young 1982). The majority of studies on tropical Lepidoptera have been on long-lived or forest inhabitants (Table 8) where hostplant availability (larval or adult resources) and predation (most often by birds) are important as primary and secondary factors determining butterfly population size (Young 1982, Ehrlich 1984, Courtney 1986, Bowers et al. 1987, Quintero 1988, Gilbert 1984, 1991). Few studies of tropical butterflies have been conducted on species that occupy non-forest habitats exclusively—only 5 of the 23 studies (7 of 42 species) in Table 8—or have been conducted on the potential predation pressure exerted by vertebrates other than birds (Boyden 1976, Ehrlich & Ehrlich 1982, Odendaal et al. 1987, Larsen 1992, Sikes & Ivie 1995). Only recently have attempts been made to quantify the selective pressure of aerial and ground-based predators on butterfly ecology and evolution (Robbins 1980, Silberglied et al. 1980, Bowers et al. 1985, 1987, Wourms & Wasserman 1985, Chai 1988, Chai & Srygley 1990, Srygley & Chai 1990, Owen & Smith 1990, Tonner et

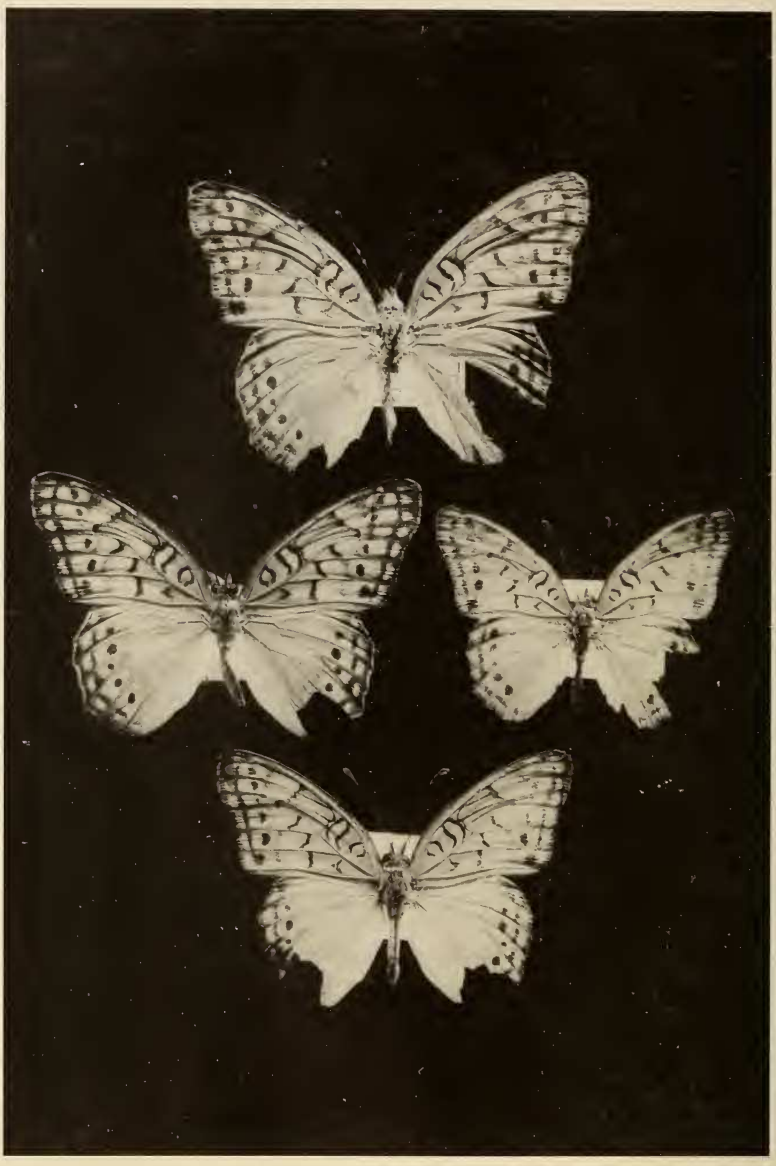

FIG. 5. Types of wing damage sustained by *E. hegesia* that may be attributable to predation. Top: female collected in 1990 with asymmetric hindwing notch thought to be the result of an attack by a bird. Middle: female (left) and male (right) collected in 1995 with asymmetric hindwing damage consistent with an attack by an *Anolis* lizard. Bottom: female collected in 1995 with symmetrical hindwing damage likely due to a single attack by an *Anolis* lizard when the butterflies wings were closed.

TABLE 8. A summary of studies of population structure and dynamics of tropical butterflies. L-P = Lincoln-Peterson, F-F = Fisher-Ford, M-P = Manly-Parr, J-S = Jolly-Seber, BTC = Bailey's Triple Catch, sample/census = actual count.

Taxon	Location	Habitat/ area surveyed	Study type	Study duration (days)	Season	Population estimator used	Population size	Sex ratio (% male)	Residence time (days)	Survival rate	Reference
Papilionidae											
Parides											
anchises										0.35–0.76	
neophilus	Trinidad	scrub	MRR	41		F-F	6–54		6	0.76–0.83	Cook et al. 1971
Parides											
proneus							756	90			
bunichus	Brazil	dry forest	MRR	305+	wet/dry	census	458	106	12		Brown et al. 1981
agavus							115	90	max. 35		
anchises							90	71			
neophilus							13	275			
Battus											
polydamas							292	72			
Pieridae											
Eurema											
daira	Costa Rica	pasture	MRR	11; 12	wet	J-S	7–9	0.60			Opler 1988
				42; 111	dry		25–78	0.91			
Nymphalidae											
Marpesia											
berania	Costa Rica	wet forest	roost census	180	wet	census	18–68	53	80	0.987	Benson & Emmel 1973
Anartia											
fatima	Costa Rica	fields	MRR / census	1–7	dry	sample	36–80				Emmel 1972
					wet	sample	14–539				
Anartia											
amalthea	Ecuador	rainforest clearing	MRR	7		L-P / BTC	78–276	27	7		Fosdick 1973
Hypolimnas											
misippus	Ghana	clearing	MRR	47–92	wet	F-F	60–650	56–86	max. 6.5	0.65	Edmunds 1969

TABLE 8. Continued.

Taxon	Location	Habitat/ area surveyed	Study type	Study duration (days)	Season	Population estimator used	Population size	Sex ratio (% male)	Residence time (days)	Survival rate	Reference
Euptoieta hegesia	Jamaica	coastal scrub	MRR	76	dry	L-P / BTC	20–400	45–122	6.5–10 max. 14	0.72–0.84	this study
Bematistes epaea							629	119			
macaria							397	311			
alcinoe	Sierra						238	170			
vestalis	Leone	wet forest	census	45		census	26	383			Owen 1974
Pseudacraea eurytus							214	30			
Acraea encedon	Uganda	savanna	MRR	335	all	L-P	10–1000	2–72	max. 16 (F) to 41 (M)		Owen & Chanter 1969
Acraea encedon	Ghana		MRR?	730	all	sample	0–160	42			Gordon 1984
Heliconius charitonius	Costa Rica	wet forest	MRR	155	wet/dry	F-F / J-S / M-P	7–139	48–76	27–42 max. 107	0.88	Cook et al. 1976
Heliconius charitonius	Puerto Rico	wet forest	MRR	300	wet	J-S	146–351	76	26 max. 70		Quintero 1988
Heliconius ethilla	Trinidad	wet forest	MRR	500	wet/dry	M-P	156	59–74	50 max. 162	0.982	Ehrlich & Gilbert 1973
Heliconius erato	Trinidad	coastal scrub	MRR	74	dry/wet	F-F			50 max. 74	0.985	Turner 1971
Placidula euryanassa	Brazil	rainforest	MRR	670	all	J-S	40–1000	42–73	7.5–8.5 max. 43		Freitas 1993

TABLE 8. Continued.

Taxon	Location	Habitat/ area surveyed	Study type	Study duration (days)	Season	Population estimator used	Population size	Sex ratio (% male)	Residence time (days)	Survival rate	Reference
Morpho peleides	Panama?	rainforest	MRR	11	dry	F-F / J-S / M-P	55–105	>50	0.94		Young 1982
Stichophthalma louisa	Burma	rainforest	MRR	32	wet	sample	150–300				Tonner et al. 1993
Satyridae											
Pierella luna	Panama	wet forest	census	146	dry/wet	census	1–7				Aiello 1992
Euptychia hermes	Costa Rica	clearing	MRR	4/5		L-P	140/184	94/70			Emmel 1970
Cissia terrestris	Trinidad	overgrown plantations	transect	variable	wet/dry	census	1–9				Singer & Ehrlich 1991
myncea							2–42				
libye							1–7				
penelope							2–56				
hesione							1–35				
renata							2–27				
hermes							7–196				
arnaea							1–21				
junia							5–26				
Danaidae											
Euploea core	Australia	dry forest	MRR	37	winter	L-P	1200–1600	108	10 max. 87	0.90	Kitching & Zalucki 1981
Amaurus niavius	Sierra Leone	wet forest	census	45		census	63	81			Owen 1974
Riodinidae											
Menander felsina	Brazil	coastal scrub	MRR	120		F-F	20		13 max. 35	0.91	Callaghan 1978

al. 1993). Here we have explored the ecology of a tropical butterfly that occupies open habitats.

Our population size estimates for *E. hegesia* over the three months at OB (approx. 200–400 individuals, Table 6) and the large number of available hosts, both *T. ulmifolia* and *Passiflora* spp., at this site suggests that relatively few plants are being used to sustain the butterfly population. Further, the clumped distribution of larvae on the primary host, *T. ulmifolia* (Table 3), suggests that some hostplants are preferred over others. The hostplants at the two small study sites (MB and SR) are more extensively used, in terms of both adult and larval population sizes, however, larval distribution at these sites is similarly non-random and clumped.

The use of single *T. ulmifolia* plants by three or more larvae, a common finding (see Table 3), is surprising considering that three larvae are capable of defoliating average size plants (Fig. 6). Plants of *T. ulmifolia* most often occur in small aggregations (likely due to limitations imposed on seed dispersal by ants; Barrett 1978), which may allow larvae to find other hosts when necessary; however, plants near to heavily preferred plants are often vacant suggesting that they are for some reason less suitable. For example, a small aggregation of six plants at OB in August contained 0, 6, 12, 12, 14 and an astounding 42 larvae per plant (Table 3) where there were no other potential hosts within 30 m in any direction. It is possible that the clumped distribution of larvae on hostplants coupled with their aposematism (and potential chemical defense based upon sequestration of cyanogenic glycosides) may afford increased protection from predation. Further, the phenotypic similarity between larvae of *E. hegesia* and *A. vanillae* and their sympatric distribution could indicate the operation of larval mimicry (Berenbaum 1995).

The high proportion of recaptures made on subsequent visits to the study sites suggests that individual *E. hegesia* are residents of specific *T. ulmifolia* populations and this appears to be the case for both large and small plant populations. Further support is provided by the lack of recaptures at the plant population just 1 km to the east of the OB site (especially given that inter-plant population movement was looked for in August when the size of the butterfly population appeared to be elevated; Table 6), and by comparison of lifespan estimates (i.e., residence time) with results of captive rearing, which suggest that average residence times span the entire life of individual butterflies. The cyanogenic status and level of intrapopulation variation of these three plant populations is relatively low (Schappert & Shore 1995) and the significance of this finding is that butterfly populations may be limited in their ability to exploit differences in the frequency of cyanogenic plants by "choosing" adjacent plant populations. The highly non-random distribution of larvae on plants also suggests that only relatively few plants in each popu-

FIG. 6. Defoliation of *T. ulmifolia* by three larvae of *E. hegesia* at Duanvale, Jamaica in 1990. Arrows show location of the larvae. Note that all that remains of the leaves are the midribs.

lation are preferred. That is, butterflies exploit differences in host quality within plant populations; however, it is not known what the basis of this choice is. Whether varying levels of cyanogenesis are responsible for this pattern is currently under investigation.

Of the population studies listed in Table 8, the most similar to our studies are those on *Anartia fatima* Godart (Nymphalidae). *Anartia fatima* has a 28–31 day life cycle, a 7–14 day average lifespan in the field (with up to 5 weeks between captures being recorded) and inhabits clearings or open areas away from the forest (Emmel & Leck 1970, Emmel 1972, Young 1972, Aiello 1992, Silberglied et al. 1980). In comparison, our study has shown that *E. hegesia* has a 28–30 day life cycle, a 7–10 day lifespan (with up to 4 weeks recorded in captivity) and similarly inhabits coastal scrub and pasture habitats away from forests. The study by Bowers et al. (1987) of predation on *A. fatima* shows that most predation, likely by birds, occurs while butterflies are at rest and the frequency of damage, interpreted to be the result of predator attack, suggested that the predation rate on adults approached 12%. They reported that males were more likely to show predator damage. Young (1972) reports that mortality in this species is high beyond early adult age classes. Although we have not directly assessed predation rate, we note that 38% of the captures in our population study, and a minimum of 32% of captures of three species of butterflies from this habitat, had sustained damage before their initial capture.

Wing damage frequencies reflect the rate of successful escapes from predators and may not reflect the actual rate of predation (Robbins 1980, Bowers et al. 1985, Owen & Smith 1990). Only if predators are 50% successful will damage or injury rates equal the predation rate. If predators are less successful or if other sources of injury are present then damage frequencies will overestimate the predation rate. Direct assessment of predator efficiency is difficult; however, Schoener (1979) proposed a method for determining predation intensity (or rate) from survival rate and injury frequency. When applied to our data (using the mean of the estimated daily survival rates; 0.632 for males and 0.612 for females) Schoener's method supports our findings that females are under greater predation intensity (i = 0.68 for males, i = 0.91 for females) and that they are damaged at almost twice the male rate (instantaneous injury rate, v = 0.22 for males, v = 0.42 for females).

The results of our studies of *E. hegesia* show that: (1) there is pronounced female-biased size dimorphism; (2) butterflies that are smaller attain a significantly greater age; and (3) in contrast to *A. fatima*, females sustain more damage that may be attributable to predators. Together this suggests that females are being removed from the population by predators. Our finding that older age classes consist of significantly smaller

butterflies suggests that selection against large butterflies, likely females, may be occurring. Our finding that females sustain significantly more total damage than males is intriguing. One possible explanation for this is that differences in the habitat where activity occurs (i.e., among vegetation for females and free-flying for males) or the type of activity (i.e., resting vs. flight) influences damage rates. For example, Moore (1987) found that mate location behavior and the activity schedule of male *Euphydryas editha* Boisduval influenced a significant bias towards male mortality for butterflies found in spider webs. Examination of the type of damage found in this study; however, shows that damage to the forewing tips and margins (which would be most expected to occur in the preceding situations) is not associated with sex. In any event, it is unlikely that symmetrical damage to adjacent wing pairs is the result of gradual wear or thrashing around in vegetation (Robbins 1980, Orive & Baughman 1989).

The lack of difference in wear (i.e., age) between sexes in this study indicates that age or "experience" is also not likely to be responsible for sex ratio biases. A capture bias towards adult males is common in butterfly population studies, and the suggestion has been that males are encountered more often and caught more easily because they are more active than females (Gall 1985). For less active females, a second explanation for female-biased damage is that damage is not related to the rate of active encounters with potential predators but to inactive encounters with ground-based predators. Ground-based predators such as *Anolis* spp. lizards may be more important to this species or, more likely, as predators in this type of habitat.

Anolis lizards commonly feed on lepidopteran larvae and adults and these often form the bulk of their diet. Floyd & Jenssen (1983) report that Lepidoptera larvae and adults account for 42% of the volume of prey found in the stomach contents—an average of three larvae or adults per anole—of *A. opalinus* Gosse on Jamaica, while Roughgarden (1995) reports that more than 36% of the volume of prey taken by *A. bimaculatus* Sparrman on St. Eustatius consisted of Lepidoptera larvae and adults. Jamaica has seven species of *Anolis* and one species of *Ameiva* and at least half of these are reported to take Lepidoptera larvae and adults as prey (Williams 1983, Schwartz & Henderson 1991). One of the species found on Jamaica, *Anolis sagrei* Duméril & Bibron, is known to take prey much larger than its body size would suggest (Schoener & Schoener 1980, Schwartz & Henderson 1991) and *A. limifrons* Cope is known to select prey larger than the most commonly available (Sexton et al. 1972).

That anoles are capable of controlling arthropod abundance has been reported by Pacala and Roughgarden (1984) and shown experimentally

by Schoener and Spiller (1987). Exclusion of anoles yielded a 2–3 fold increase in insect abundance and a 20–30 fold increase in the abundance of web-building spiders on St. Eustatius (Pacala & Roughgarden 1984). Interestingly, web-building spiders are themselves predators of butterflies (pers. obs., Moore 1987). Removal of *A. sagrei, A. carolinensis* Voigt and *Ameiva festiva* Richtenstien & von Martens from experimental plots in the Bahamas resulted in spider—and spider prey—densities 2–3 times higher than that found in control plots (Schoener & Spiller 1987). Roughgarden (1995) suggests that anoles fill the niche of ground-feeding birds that are absent from the Caribbean islands, and notes that anoles often attain very high densities. Schoener and Schoener (1980) reported densities of *A. sagrei* in the Bahamas approaching 1 per m^2. Four of the seven species of *Anolis* known from Jamaica occur at OB and if their combined density is 1 anole per m^2 then some 200,000 anoles may be present at this site.

A few studies have documented the potential importance of lizards as predators of butterflies (Boyden 1976, Ehrlich & Ehrlich 1982, Odendaal et al. 1987, Owen & Smith 1990, Larsen 1992). From our experience with *Anolis lineatopus* Gray preying on captive females in an oviposition enclosure, and experimental presentations of larvae to this species, at Discovery Bay, St. Ann, we would suggest that lizards may be important predators in this system. Despite extensive time in the field we have not seen birds preying on this species, although one specimen of a series of 30 adults taken at OB in June 1990 shows an obvious beak mark (a triangular notch) on the right hindwing (see Fig. 5). Predation by birds is well documented for this and many other species (Bowers et al. 1985, Wourms & Wasserman 1985, Chai & Srygley 1990). Two common species of insectivorous birds occur at OB: the Loggerhead Kingbird, *Tyrannus caudifasciatus* (D'Orbigny) and Northern Mockingbird, *Mimus polyglottos* L.

A variety of other predators are expected, or have been reported, to attack *E. hegesia*. Alonso-Meija and Marquez (1994) report dragonflies preying on various species of butterflies in Costa Rica including *E. hegesia*. Chai and Srygley (1990) reported that 8 of 10 *E. hegesia* offered to a captive bird were attacked and consumed. Interestingly, neither Hallman (1979) nor our studies have found parasitoids in larvae or pupae although Hallman noted their presence in more than 60% of eggs from Colombia. The absence of parasitoids in this species is remarkable; however, our estimate of mortality rate in Jamaican *E. hegesia* is extraordinarily high. Given that the actual sex ratio is 1:1 and that females lay, on average, 27 eggs per day, then 200 females at OB could produce 5400 eggs per day and a stable female population will produce about 37,800 eggs each week. Further, given that the average lifespan in captivity is

about 7 days (and estimates of residence time from this study agree with this figure), and assuming a stable adult population of approximately 400 butterflies, then about 37,400 eggs, larvae, and pupae do not survive to become adults. This suggests that mortality of these stages approaches 99% or more.

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